

ON THE BIONOMICS, ANATOMY, AND SYSTEMATICS OF
WAGNERONOTA (COLEOPTERA: MELOIDAE)

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Abstract.—Some aspects of the bionomics of *Wagneronota aratae* (Berg), including male courtship behavior, are described from observations made in Catamarca, Argentina. The species is widely distributed in northwestern Argentina, where adults feed on the leaves and flowers of *Zizyphus mistol* (Rhamnaceae) and, occasionally at least, invade potato fields. The pattern of courtship behavior is basically like that of *Pyrota*. The triungulin larva has hypertrophied, extended spiracles on abdominal segment I, a specialization paralleled in the nemognathine genus *Tetraonyx* and in an unidentified Asian *Meloe* but previously unknown in the tribe Lyttini. In the adult stage *Wagneronota* is the largest of the Meloidae, reaching a maximum length of 4½ cm. The larger of two egg masses obtained from captive females (4220 eggs) is, numerically, the largest recorded for a coleopteran. On the basis of behavioral and anatomical characters, Kaszab's assignment of *Wagneronota* to a systematic position near *Pyrota* in Pyrotina is amply confirmed.

Wagneronota aratae (Berg) enjoys the distinction of being, as an adult, by far the largest of all blister beetles and, it seems to me, one of the most handsome. In addition, it may well prove to have the greatest fecundity of any coleopteran. Although named a century ago and familiar to several generations of Argentine and foreign entomologists, the species has nevertheless remained poorly studied anatomically and virtually unknown bionomically up to this time. In this work, intended as the first in a series treating the Latin American lyttine-pyrotine complex of genera, I summarize available distributional data, record recent behavioral observations, describe the egg and triungulin larva, redescribe the adult, and discuss the systematic position of *Wagneronota*.

BIONOMICS

Geographic distribution.—Northwestern Argentina, from Jujuy and Santiago del Estero to Mendoza and San Luis, at low and moderate elevations (2000 m or less) (Fig. 1). The following records are available:

ARGENTINA: *Catamarca*: (DEI, MLP) 6 (1 labeled II-87); Andalgalá, 28-I-60, Willink & Tomsic (IML) 1; Belén, III-39 (IML) 3; Belén to Andalgalá, III-39 (FGW, IML) 2; same, no date (IML) 1; Hualfin, 3-I-49, Ares (IML) 1; 5 km N Santa María, 1900 m, 14-II-83, Selander & Peña (RBS) 28. *Córdoba*: Guanaco Muerto, X-72, Martínez (AM) 1. *Jujuy*: (Bosq, 1943). *La Rioja*: (AM, BM, IML)

8; Mascasín, XI-61, from Walz (RBS) 20, II-64, Martínez (AM) 5. *Mendoza*: (BM, MLP) 3. *Salta*: (MLP) 1; San Carlos, 21-I-50, Monrós (IML) 1. *San Juan*: (MLP) 1; Astica and Usno (Viana and Williner, 1973). *San Luis*: San Gerónimo (Viana and Williner, 1972). *Santiago del Estero*: 25-II-47, Meyer (IML) 4; no date, Wagner (MLP) 1; Campo Grande, III-43 (AM) 1; Fernández, II-58, from Walz (RBS) 8; Fries, I-52 (AM) 1; Icaño, Wagner (MLP) 10; Río Salado, Kohler, Mason (BM, FREY, MLP, USNM) 8; Sumampa (Villa Union), X-44, Prosen (AM) 1. *Tucumán*: (MLP) 2; Amaicha del Valle, 1978 m, 23/27-XII-64, Selander & Storch (RBS) 2, 1-II-64, Heller (IML) 1. *Country label only*: (BM, FREY, IML, MLP) 7.

Seasonal distribution.—Adults have been collected from October to March. Three-fourths of the records fall in the period January–March.

Habitat and feeding behavior.—The only food plant recorded previously is potato (*Solanum tuberosum*). According to Bosq (1943), adults are found “frequently in plantings . . . , eating the leaves.” Hayward (1960) reported damage to potato plants in Tucumán. But despite these reports, the species apparently does not invade potato fields with any regularity, since it is not mentioned in any of several Argentine works devoted to potato pests (e.g., Blanchard, 1929). Two adults (male and female) that R. Storch and I took at light in Amaicha del Valle, Tucumán, in 1964 refused both *Solanum elaeagnifolium* and lettuce.

On the afternoon of 14 February 1983, while collecting with me near Santa María, Catamarca, Luis Peña called my attention to an adult of *Wagneronota aratae* feeding on a flower of a small tree later identified as representing *Zizyphus mistol* (Gris.) (Rhamnaceae). This plant, commonly called *mistol*, is widespread in northwestern Argentina, where it is well known as a source of edible fruit, medicinal products, and wood (Alvarez, 1919). In the Santa María Valley we found it restricted largely to the flood plain of the Río Santa María and adjacent low, sandy areas supporting xerophytic vegetation. For several days we had collected from this plant more or less casually, taking *Epicauta atomaria* (Germar) and a similar, unidentified *Epicauta* in small numbers. Stimulated by Peña's discovery, we now began to examine *Zizyphus* trees in earnest and shortly found a population of 70 *Wagneronota* in a small tree, near a cultivated field (Fig. 2).

The beetles were distributed from the top of the tree (at about 5 m) to middle height, for the most part in dense groups. Both here and in captivity they freely permitted contact with other individuals. Their first response when approached was to hold still; subsequently they began to crawl over the vegetation, and about 10 individuals took to flight, heading downwind at heights of 5–7 m. Later the same day we returned to the tree and observed the remaining beetles (about 30 in all) until dark. At first they were concentrated in two compact groups, often standing on each other, with very little movement, and that quite leisurely. As it grew darker, individuals began to clean themselves and then to move out, crawling up the stems and occasionally nibbling on a leaf or flower. There was no courtship earlier in the day or at this time. At 8:30 pm we turned on the car lights, close to the tree, but none of the beetles was attracted to the lights. The next morning only a single adult remained in the tree, and it had left by the afternoon of the next day. On that afternoon I made a transect running a mile north from the tree, examining about 75 *Zizyphus* trees for *Wagneronota* without success. Considering the apparently low population density of adults in the area and their highly



Fig. 1. Geographic distribution. Open circle represents a provincial record.

gregarious behavior, it would seem that we had been decidedly fortunate in finding even one group.

The sample of adults obtained near Santa María was maintained in captivity for two weeks with virtually no mortality on a diet of *Zizyphus* leaves and flowers.

Grooming.—The antenna is cleaned by passing it through the mouthparts. This behavior involves trapping the antenna in the angle between the forefemur and foretibia, bringing the foreleg in front of and slightly below the mandibles, and



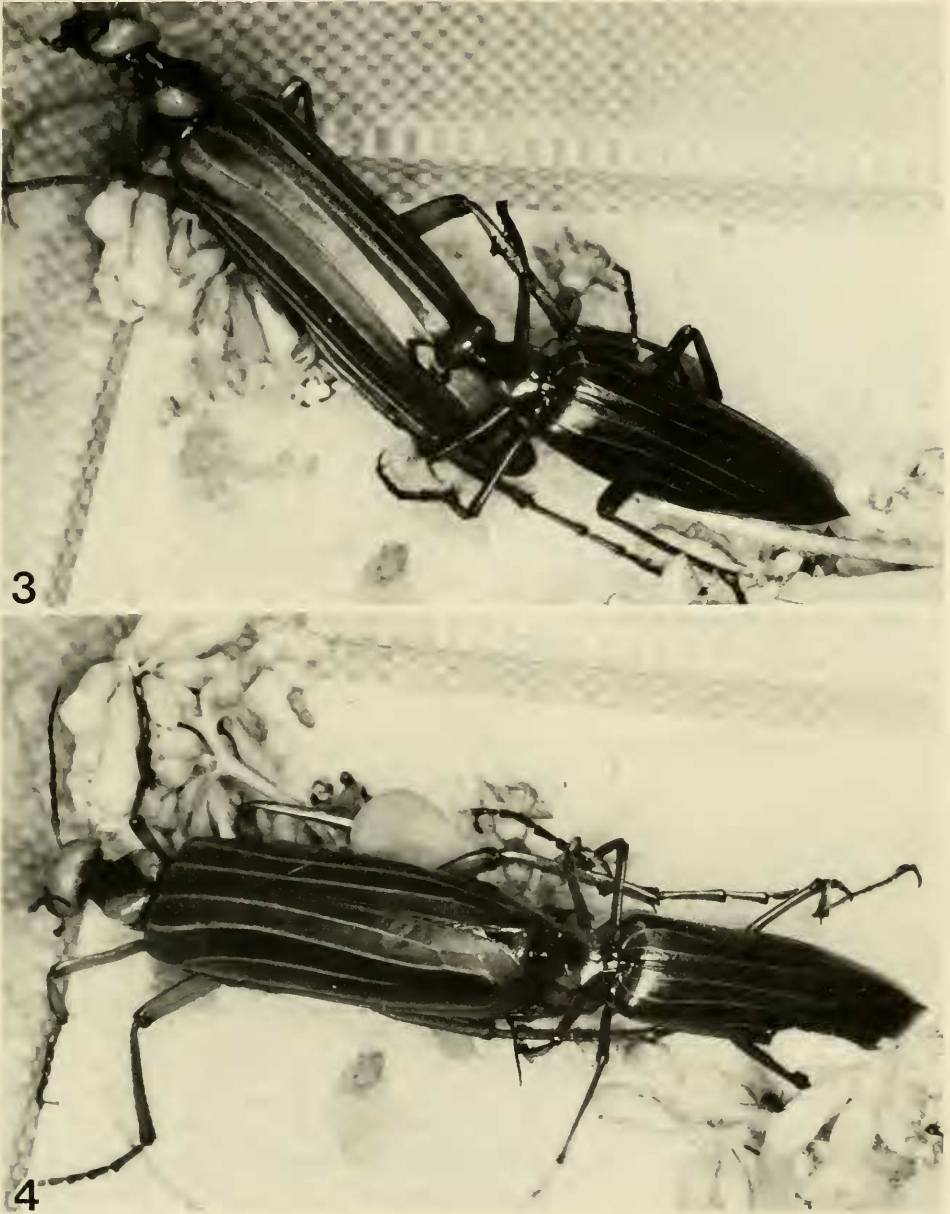
Fig. 2. *Zizyphus mistol* tree that supported a large aggregation of adults of *Wagneronota aratae* in the Río Santa María Valley, 1900 m, Catamarca, Argentina. Chilean entomologist Luis E. Peña in the foreground.

holding it there to brace the antenna as it passes from base to apex through the mouthparts. The elytra are cleaned by brushing the mid- and/or hindlegs over them. The forelegs clean the other legs and are then cleaned with the mouthparts.

Courtship.—Although some of the beetles were feeding in the afternoon when we first found them, in captivity they were almost totally inactive in the presence of light. Yet when the light in the room was extinguished at night we could soon hear the beetles moving about in their cages, and by leaving them in the dark for an hour or more and then turning on the light I was able to observe and photograph courtship, feeding, and other behavior.

In all I observed perhaps 20 bouts of courtship behavior, largely involving females which were disturbed and moving. None of the bouts lasted more than a few minutes after observation began and none led to copulation. Under the circumstances, my observations are sufficient only to establish some of the more obvious features of the behavior, and in particular the positional relationships of the male and female.

The male remains fixed behind the female, with his head at or near the end of her elytra. From this position he grasps each of her hindtibiae with his corresponding forelegs by pinching the tibia between the fourth and fifth tarsal segments. Often he holds the middle of the tibia, but the grasp may be made at or near the base or slip to that position from the middle. The male's mid- and hindlegs generally remain on the substrate, but I occasionally saw a male grasp the female's hindtibiae with the midtarsi as well as the foretarsi. Initially and later, during interruptions of antennation, the male's antennae are directed diagonally forward.



Figs. 3-4. Courtship behavior. 3, Male in usual position behind female. 4, Male with head inserted under female's elytra.

Once in position the male lowers the head and presses the mouthparts on the female, with the maxillary palpi spread to the sides and in extensive contact with her elytra or abdomen. The antennae are then folded at the joint between segment I, which projects forward and down, and segment II, directing the flagella obliquely back and down, where they are vibrated rapidly against the female in extended bouts (Fig. 3). Initially and periodically thereafter the male tries to insert the

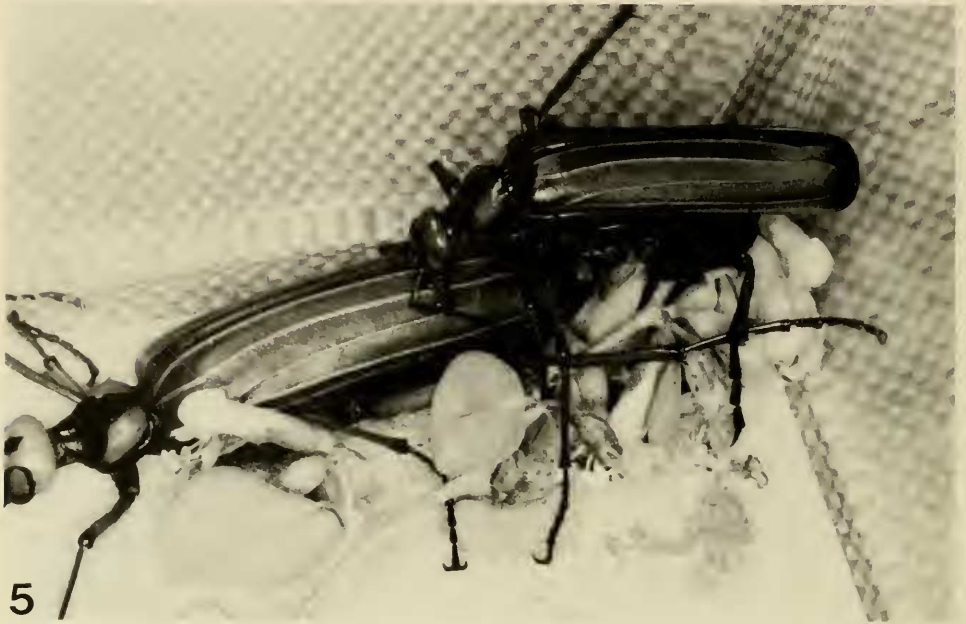


Fig. 5. Courtship behavior, showing beginning of abdominal curvature.

mouthparts under the ends of the female's elytra, evidently in an effort to make palpal contact with the dorsum of her abdomen. Rarely the entire head was thrust under the female's elytra (Fig. 4). While antennation is in progress, the male curves the abdomen forward (Fig. 5), eventually bringing the apex of his genitalia to the tip of the female's abdomen, where it is held at least momentarily. In a few cases I detected a single genital stroke, in which the end of the abdomen was brought under the female's abdomen and then brushed back over the last one or two sterna, before the actual genital presentation.

Antennation was continuous during both abdominal curvature, stroking, and genital presentation. Commonly the female moved her legs or body in response to genital presentation, interrupting the male's behavior.

In none of my observations did the male mount the female or touch her with the antennae when they were extended forward. Nor did he ever release his grasp of the female's hindtibiae while courtship was in progress. I suspect that genital presentation occurs cyclically when the female is relatively calm and sedentary and that, as part of the cycle, antennation is periodically either modified in form or spontaneously interrupted.

So far as observed, the courtship behavior of *Wagneronota* is very similar to that of species of *Pyrota* Dejean (Selander, 1964). The principal distinctive features of *Wagneronota* are (1) ability and apparent willingness of the male to perform antennation and genital presentation without inserting the mouthparts beneath the female's elytra and (2) the apparent lack of a mounted phase of courtship, in which the male releases the leg grasp, moves forward over the female, and antennates and palpates her body from a fully mounted position.

The male's foretarsal grasp is facilitated by modifications of the last two segments of the tarsus described and illustrated by Denier (1932), who conjectured

(wrongly) that they might be adaptive in manipulating the female's antennae. Modifications of the male's antenna and maxillary palpus are relatively slight. The antenna is longer and thinner than in the female. The last two segments of the maxillary palpus are a little enlarged and are flattened ventrally, but membranous, densely setate areas, present ventrally on one or both of these segments in most species of *Pyrota*, are lacking. Since rubbing of the palpi over the elytral surface of the female is a conspicuous feature of the mounted phase of courtship in *Pyrota*, the weakness of the modification of the palpus in *Wagneronota* might be interpreted as evidence that the phase is absent. However, some species of *Pyrota*, such as *P. mutata* Gemminger, with no stronger modification of the palpus than in *Wagneronota* nevertheless have a fully developed mounted phase. As in *Pyrota*, the posterior margin of the male's last visible abdominal sternum is turned dorsad distally, evidently as an adaptation for genital presentation from directly behind the female.

Response to contact.—As indicated above, the adults commonly rest and feed in proximity to each other. In such situations and in other encounters there was no suggestion of antagonism among them. Physical contact with conspecifics seemed to be ignored generally, although I occasionally saw an individual lower the head and antennae when another one walked over him. Yet throughout the period that I kept adults in captivity they remained unusually sensitive to foreign stimuli, both visual and tactile. As an example of this sensitivity, a male that I touched lightly with my finger remained absolutely motionless for 20 minutes. When handled roughly adults "feigned death," flexing the legs (but not drawing them in closely to the body) and occasionally producing droplets of yellow fluid at the femorotibial joints.

Eggs.—Captive females produced four egg masses, two of which I recovered intact. The eggs are subcylindrical, tapered moderately from the middle to the posterior end, and blunt at both ends. The color is pale yellow. Mean length in a sample of 7 unhatched eggs was 1.37 (.013) mm and mean width .37 (.003) mm. Estimated egg volume, applying the formula for the volume of a cylinder, is .144 mm³. The eggs have a sweet, perfume-like odor that was immediately detectable when the cages in which they were laid were opened. I have noted the same or a very similar odor in vials of eggs of several species of *Epicauta*.

The two intact egg masses of *Wagneronota* contained 3780 and 4220 eggs, respectively. Numerically, the latter mass is by far the largest recorded for a meloid. The previous record for a single oviposition was 3854 eggs, laid by a female of *Meloe laevis* Leach (Pinto and Selander, 1970). Unless the adult life of *Wagneronota* is unusually short for a meloid, and there is nothing to suggest that it is, the total number of eggs produced by a female of *Wagneronota* probably exceeds that of any other beetle.

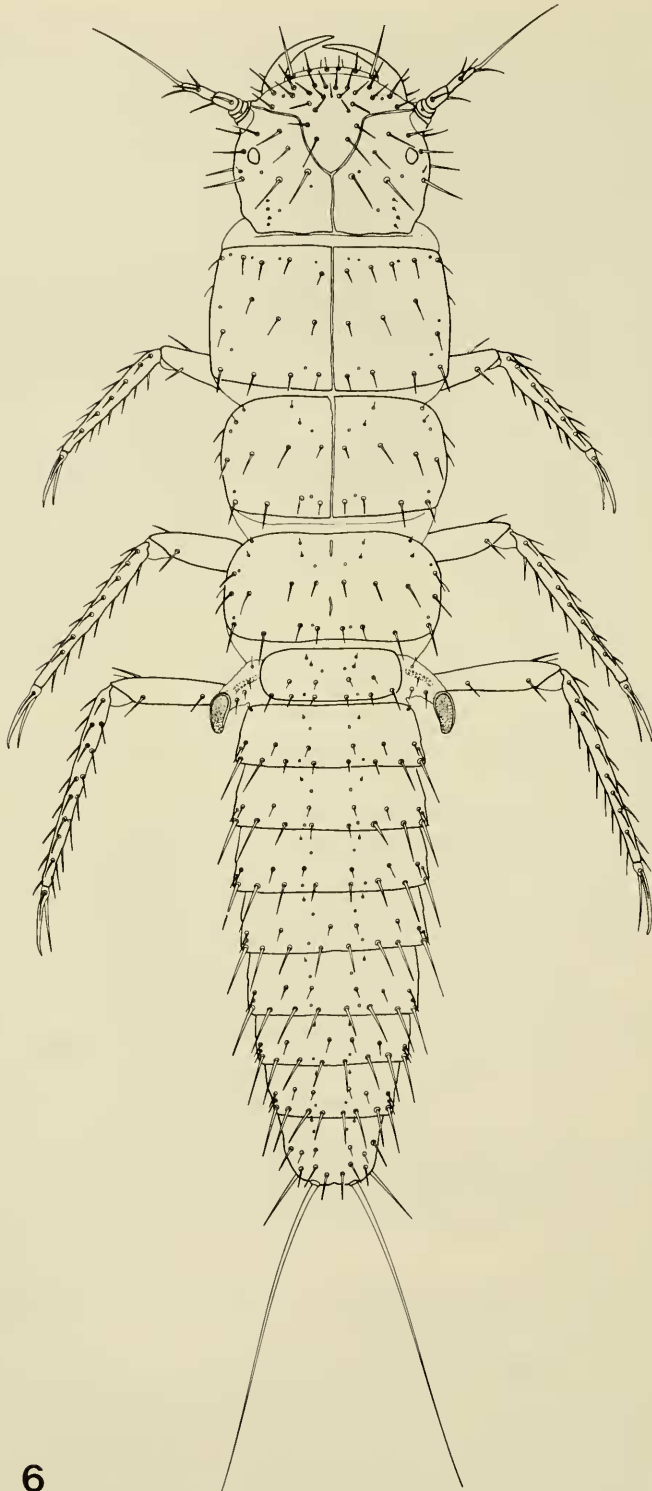
Incubation time, at ambient temperature and 100% RH, was 12 days for three egg masses in which hatching occurred.

DESCRIPTION OF TRIUNGULIN LARVA

Figs. 6–8

Color uniform light brown. Cuticle of posterior dorsal surface of head and anterior $\frac{1}{3}$ of meso- and metanotum distinctly reticulate; reticulations coarse, transverse.

Head transversely oval, nearly $1\frac{1}{4} \times$ as wide as long. Epicranial suture complete



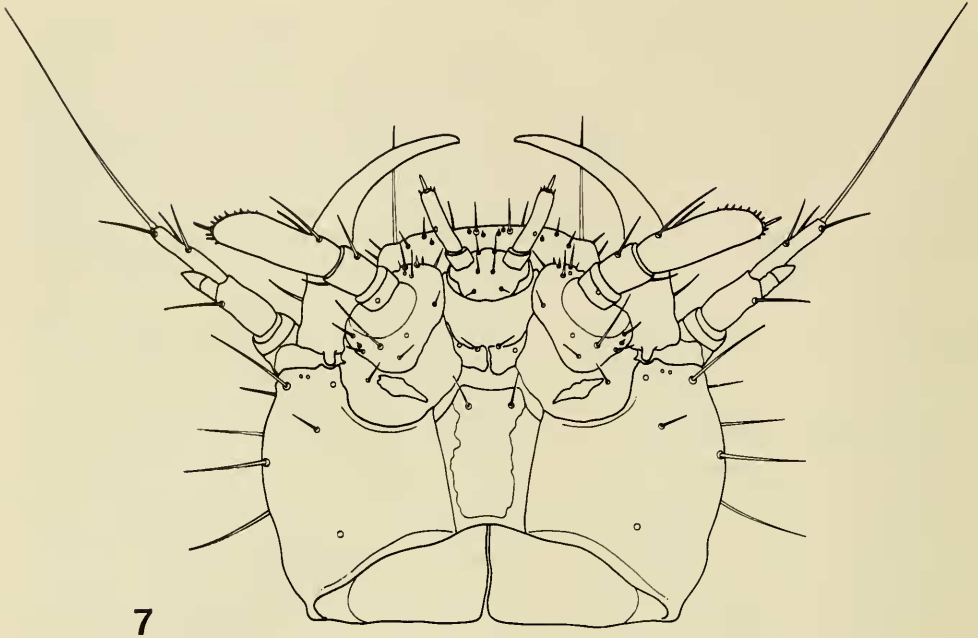
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Fig. 6. Triungulin larva, dorsal view.

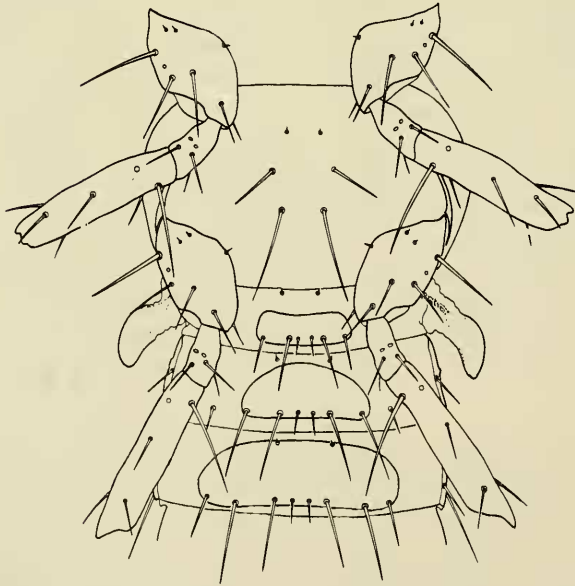
to base of mandible; stem about $\frac{1}{3}$ as long as head. Six major setae on posterior dorsal surface of head; these and major lateral setae on each side about $\frac{1}{4}$ as long as head. Front with 4 setae between arms of epicranial suture before they turn laterad; transverse row of 8 setae between antennae and similar row of 8–9 setae on anterior margin. Clypeus with similar median transverse row of 8 setae. Gula longer than wide; anterior margin projecting well anteriorly of anteroventral margin of head capsule; gular setae surpassing anterior gular margin. Labrum well sclerotized, only partially recessed, about $\frac{1}{2}$ as wide as head; six dorsal marginal (DM) setae; DM₁ short; ratio of lengths of DM₁, DM₂, and DM₃ 1:1.5:3.5; DM₃ as long as maxillary palpal segment III. Eye small, slightly longer than wide; greatest diameter equal to width of maxillary palpal segment II. Mandible slender, lacking teeth, $\frac{7}{10}$ as long as head. Antennal segment I short, $1\frac{3}{4}\times$ as wide as long; II $2\times$ as long as wide, $2\frac{1}{4}\times$ as long as I, with 2 setae, which are nearly as long as segment; sensory appendix long, slender, acute, about $\frac{3}{5}$ as long as II, its basal $\frac{1}{3}$ a membranous tube; cone itself $\frac{3}{5}$ as long as wide; III slender, $5\times$ as long as wide, $1\frac{1}{2}\times$ as long as II, with 3 setae like those on II, terminal seta $2\frac{3}{5}$ as long as III. Maxilla with seta of cardo in membrane, not on sclerite; mala ventrodistally with 2 moderately long setae, 1 short seta, and 1 cone-like, 2-segmented sensory appendix, dorsally with 4 setae along median margin and 2 along distal margin. Maxillary palpus large, prominent; segment I short, about $\frac{3}{4}$ as long as antennal segment I, $2\times$ as wide as long; II as wide as long, $2\times$ as long as I, with seta on each side, about as long as segment; III nearly $3\times$ as long as wide and nearly $3\times$ as long as II, basally with long mesolateral and 2 dorsal setae, all attaining sensory area or nearly so; sensory area of III oblique, extending to distal $\frac{2}{5}$ of segment, set with 40 large papillae (cone-like setae); 2-segmented sensory appendix very long, slender, $\frac{1}{5}$ as long as segment. Labium with prementum II divided on midline, each half with short seta and sensory pit; prementum I with 3 pairs of setae ventrally and anterior marginal row of 4 short, stout setae dorsally. Labial palpus elongate, slender; segment I as wide as long, as long as maxillary palpal segment I; II cylindrical, slightly curved, $3\times$ as long as wide, $3\times$ as long as I, with 2 dorsobasal setae, nearly attaining apical sensory area; apex of II with 7 short setae, 5 of these on oblique dorsal sensory area; 2-segmented sensory appendix of II about $\frac{3}{10}$ length of segment, $2\times$ as wide as appendix on maxillary palpal segment III.

Thorax with line of dehiscence complete on pro- and mesonotum, faintly indicated, discontinuous on metanotum; setae short or of moderate length. Pronotum rectangular, $\frac{3}{5}$ as long as wide, nearly as long, and more than $1\frac{1}{2}\times$ as wide, as head; 28 major setae, roughly in 3 rows; posterior (marginal) row (PR) with 8 setae; PR₃ and PR₄ more than $2\times$ as long as PR₁ and PR₂. Meso- and metanotum oval, about $\frac{1}{2}$ as long as wide, slightly narrower than pronotum. Mesonotum with 20 major setae, primarily in 2 rows; lateral setae longer than median setae; PR with 8 setae. Prosternum with paired setae in anterior (AR), median (MR), and posterior (PR) rows long; ratio of lengths of AR₁, MR₁, and PR₁ 1:1:1.8; AR₁ slightly longer than maxillary palpal segment III. Meso- and metasternum with setae AR₁ tiny; MR₁ and PR₁ slightly longer than counterparts on prosternum.

Abdomen with sterna of all segments heavily sclerotized; pleurites separated from tergites by very fine suture; tergites with setae in median row (MR) short; median setae in MR and PR shorter than lateral ones, difference progressively



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Figs. 7-8. *Triungulin* larva. 7, Head, ventral view. 8, Metathorax and abdominal segments I-III, ventral view.

less marked posteriad. Segment I with spiracle greatly enlarged, located on prominent lateral, membranous, tubular extension of segments; tube with 3 dorsal setae; atrium funnel-shaped, lined with hexagonal cellular reticulation; peritreme pyriform; tergite I narrower than rest, with only 4 setae in MR and only 6 in PR;

ratio of lengths of PR₁, PR₂, and PR₃, roughly 1:2:4. Sternite I narrowed, rectangular, 2× as wide as long, with only 6 setae in PR; PR₂ longer than PR₃, more than 2× as long as PR₁. Segments II–VIII similar to one another in form and setation; tergites with 8 setae in MR and 8 in PR; MR₄ caudad of others in MR, near base of PR₄; 2 setae (1 marginal) on pleurite, both large; sternites with 8 setae in PR. Tergite V $\frac{3}{10}$ as long as wide, ratio of lengths of setae PR₁, PR₂, PR₃, and PR₄ about 1:1.3:1.6:1.7; PR₄ $\frac{3}{4}$ as long as tergite. Sternite II narrowed, with seta PR₄ in membrane laterad of sternite; setae on sterna III–VIII all on sternites. Sternite V nearly $\frac{2}{5}$ as long as wide; ratio of lengths of setae PR₁, PR₂, PR₃, and PR₄ about 1:2.3:2.3:1.3; PR₂ as long as sternite. Segment IX with row of 10 long setae ventrally at anus; caudal seta $5\frac{1}{2}$ × as long as tergite V; adjacent large seta $\frac{1}{5}$ as long as caudal seta.

Mesothoracic spiracle smaller in diameter than eye; abdominal spiracles II–VIII subequal to one another in diameter, $\frac{1}{2}$ diameter of mesothoracic spiracle.

Legs long, slender, without lanceolate setae. All segments of legs II and III noticeably longer than those of leg I; tibia III nearly $1\frac{1}{2}$ × as long as tibia I. Ratio of lengths of femur, tibia, and tarsungulus 1:1.2:0.5 on leg I, 1:1.5:0.4 on leg III. Femora with ventral major seta set near base. Tarsungulus with ventral (bladlike) seta nearly attaining apex.

Body length 2.0 mm; caudal seta length .55 mm.

Remarks.—In numbering the setae in a transverse row I follow my previous convention (Selander, 1982) of counting from the midline of the body.

If one ignores the shape of the gula, *Wagneronota* keys to *Pyrota* in MacSwain (1956). Moreover, it agrees in nearly every character with his diagnoses of the tribe Pyrotini (which I prefer to regard as a subtribe of Lyttini) and genus *Pyrota*. MacSwain's (1956) study included only three pyrotine species, all belonging to *Pyrota*. Since his study appeared I have obtained the larvae of 11 additional species of *Pyrota*, and on the basis of these and the larva of *Wagneronota aratae*, I would modify MacSwain's diagnosis of the Pyrotina to read as follows:

Labrum at least partially recessed beneath head. Mandible slender, lacking teeth. Antennal segment II long, much longer than wide. Abdomen with fine suture between tergites and pleurites. Abdominal tergites II–VIII with 8 setae (not 6 as stated by MacSwain) in median row; lateralmost seta (MR₄) caudad of others, near base of PR₄. Abdominal sternum well sclerotized, with large, undivided sternite on each of segments I–IX; sternite I with setae of PR reduced from 8 to 6; II with seta PR₄ in membrane at side of sternite. Abdominal spiracle I much larger than others on abdomen, dorsal, on tergite; spiracles II–VIII lateroventral, on pleurites. Legs without lanceolate setae.

Among the many differences between *Wagneronota* and *Pyrota*, the following are noteworthy: In *Wagneronota* (1) the gula is elongate; (2) the maxillary palpus is enlarged; (3) there are fewer setae on the dorsum of the epicranium and on the thoracic nota and fewer (8 rather than 10) in the PR of abdominal tergites II–VIII; (4) in the PR of the thoracic nota and abdominal tergites the median setae are shorter than the lateral setae; and (5) abdominal spiracle I is hypertrophied and located on a lateral extension of the abdomen.

There is nothing in *Pyrota* comparable to the elaboration of abdominal spiracle I in *Wagneronota*. Marked hypertrophy and extension of this spiracle is, however, characteristic of the nemognathine genus *Tetraonyx* Latreille (MacSwain, 1956)

and an unidentified species of *Meloe* Linnaeus from Turkestan described by Zakhvatkin (1932). In all three cases the enlarged peritreme is connected to the trachea by a deep funnel-shaped atrium, the sclerotized surface of which is strongly reticulate. The reticulation in *Wagneronota* forms what appear to be hexagonal cells but are actually deep cups, each containing a blunt median papilla. In the *Meloe*, judged from Zakhvatkin's work, the pattern is precisely the same. Zakhvatkin illustrates this pattern also for the mesothoracic spiracle and abdominal spiracle III, and it is present in at least the mesothoracic spiracle of *Wagneronota* (I cannot determine the nature of the atrial lining of the small spiracles on abdominal segments II–VIII). In many species of *Tetraonyx* the atrium has a similar, cellular structure but the cups lack median papillae; in other species the reticulation takes the form of large rectangular cells, with a row of long setae or spines lining the atrium internally near its middle. On all tracheal branches leading to abdominal spiracles in *Wagneronota* there is a sclerotized bar or lever that is evidently capable of pinching off the trachea. What appears to be essentially the same mechanism was described and figured for the *Meloe* larva by Zakhvatkin. Both *Wagneronota* and the *Meloe* retain the full complement of abdominal spiracles; in *Tetraonyx* spiracles II–V are unusually small and VI–VIII have been lost (MacSwain, 1956).

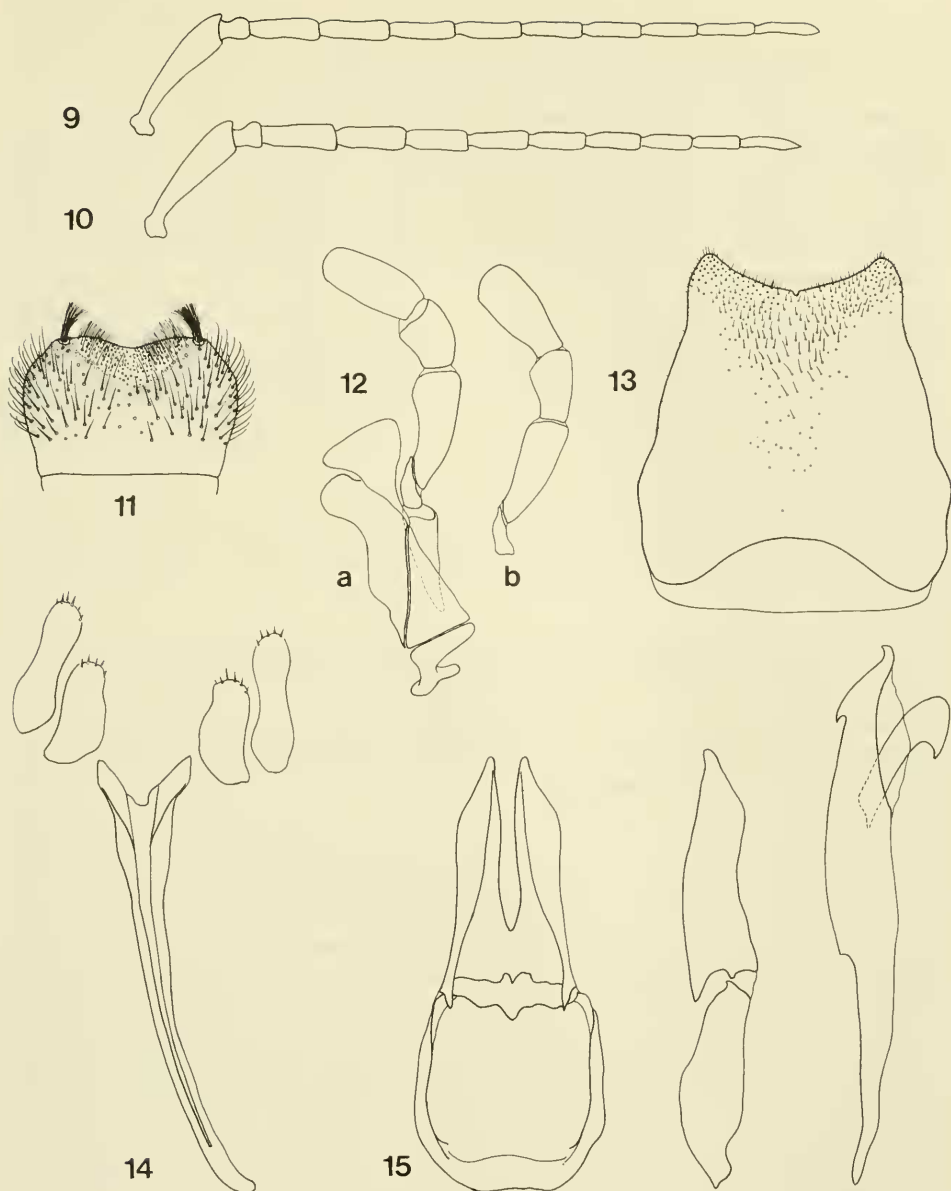
In *Meloe* the spiracular extension is apparently consolidated with abdominal tergite I. In *Tetraonyx* the extension, although itself sclerotized externally, arises from a membranous lateral area of the abdomen. In both genera the extension is just large enough to contain the enormous atrium. In *Wagneronota* the extension is only partially filled by the atrium and is sclerotized only in the distal region surrounding it, thus allowing for, presumably, considerable amplitude of movement. In this genus, at least, it is evident that the extension has some function other than accommodating the atrium.

While both *Meloe* and *Tetraonyx* are phoretic as triungulins, hypertrophy of abdominal spiracle I is apparently not directly adaptive in phoresy, since *Wagneronota* is non-phoretic. Because of its open form, it seems unlikely that the atrium guards the trachea against dust or pollen grains. One possibility worth investigating is that the atrium is capable of trapping an air bubble. In larvae feeding on liquid provisions of a host bee this might provide a temporary supply of oxygen and prevent flooding of the trachea if the abdomen were submerged in the food.

DESCRIPTION OF ADULT

Figs. 9–15

Head largely orange; median spot on vertex, anterior $\frac{1}{2}$ of clypeus, narrow margin around eye, and entire underside of head black; black spot on vertex rarely expanded to fuse with eye margining. Labrum, mandibles, antennal segments I–II, maxillary palpus, and last segment of labial palpus orange, finely margined with black. Antennal segment III piceous; rest of flagellum black. Pronotum black in anterior $\frac{1}{2}$, orange in posterior $\frac{1}{2}$ except along margins and on disk, where anterior black area extends posteriad as a broad triangle nearly reaching basal margin. Scutellum black. Elytra immaculate orange-brown. Hind wings dark brown, with apical region and posterodistal margin pale. Legs, except for piceous forecoxa, orange, often darker than head and pronotum. Venter of body black except last



Figs. 9–15. Adult anatomy. 9, Antenna, male. 10, Antenna, female. 11, Labrum, female. 12, Maxilla, male (a), and maxillary palpus, female (b), ventral views. 13, Sixth (visible) abdominal sternum, male, ventral view. 14, Abdominal segment IX, male, dorsal view. 15, Genitalia, male (ventral and lateral views of gonoforceps, lateral view of aedeagus).

2 visible abdominal segments deep orange and preceding 2 sterna with an orange lateral spot. All clothing setae except minute erect setae on head and elytron black. Length 18–45 mm, usually 30 mm or more.

Head quadrate; greatest width above eyes about $\frac{9}{10}$ length (to base of labrum); dorsal margin rounded; tempora poorly defined; median sulcus poorly developed;

vertex flattened above eye; front flat; antennal callosity small, hardly elevated; cuticle of vertex and front of head very shiny, smooth, with few very small, scattered punctures, superficially glabrous but actually with minute seta in each puncture; underside of head sparsely, very finely punctate, with erect setae of moderate length. Labrum finely, sparsely punctate, emarginate, with conspicuous, dense tuft of setae on each side of emargination. Maxilla with galea broadly triangular; lacinia rounded; palpal segments moderately heavy, not elongated. Labium with segment III unusually small, glabrous. Eye very large, broad, prominent. Antenna slender, extending several segments beyond base of pronotum; segment I much longer than others, becoming progressively thicker distad; flagellum filiform, with segments elongate, compressed. Neck densely punctate.

Pronotum $\frac{1}{10}$ as wide as long; sides rather evenly convergent from middle to apex, with distinct subbasal angle, often produced as a massive spine; disk weakly concave in apical $\frac{1}{3}$, flat elsewhere; cuticle as on vertex, with center of disk nearly impunctate. Scutellum small, rounded apically; exposed portion impunctate.

Elytron with 3 strongly elevated costulae; cuticle much less shiny than head and pronotum, densely, finely punctate, superficially glabrous but actually with minute, widely scattered setae; intervals between punctures microgranulate and punctulate.

Thorax with venter very finely punctate, clothed with long, fine black setae which are apparently easily lost through abrasion; mesepisterna distinctly separated on midline, each with well defined marginal area which is moderately tapered medianly but not acuminate. Abdominal sternum sparsely, very finely striopunctate, with fine, short setae; fifth (visible) sternum broadly, shallowly emarginate. Pygidium shallowly emarginate.

Legs long, slender, for most part sparsely setate. Tibiae straight, not bowed; posteroventral margin of foretibia pubescent, densely lined with recumbent, sericeous setae; dorsal edge of midtibia densely lined with short, coarse, setae of uniform length. Fore- and midtibial spurs slender, spiniform; hindtibial spurs thickened, outer one especially so, at least $2\times$ as wide as inner spur; both spurs obliquely truncate, apically acute. Tarsi laterally compressed; segments not bilobed; pads (pale ventral pubescence) well developed, dense, parted on foretarsus, finely divided on midtarsus, broadly divided on hindtarsus; claws not denticulate.

Male.—Eye larger and proportionately wider than in female. Antenna longer; segment I and flagellar segments more elongate in form; basal flagellar segments tending to be weakly curved. Maxillary palpus with segments III and IV somewhat shortened, flattened ventrally but not otherwise modified. Sixth (visible) abdominal sternum with posterior margin turned abruptly dorsad, providing an extensive, sclerotized vertical surface between prominent, divergent, angulate lateral lobes; dorsal margin fringed with setae; segment IX as in Fig. 14. Genitalia as in Fig. 15; aedeagus with 2 well developed hooks; dorsal hook massive. Legs longer than in female. Foretarsus moderately swollen; last segment strongly curved, with pad rounded, confined to base of segment; ventrolateral slots in segment widened and deepened, providing for extreme flexure of tarsal claws.

Female.—Sixth abdominal sternum truncate, with shallow depression on midline in posterior $\frac{1}{2}$.

Remarks.—In addition to genitalic characters and modification of the male's foretarsi for grasping the female's hindlegs in courtship, the male differs from the

Table 1. Comparison of anatomical ratios in males and females. For each sex, N = 10.

Ratio ^a	Males		Females		t	P
	Mean	SE	Mean	SE		
Head: W/L	.91	.010	.93	.008	-1.603	.126
MDE/Head W	1.07	.007	1.03	.007	3.710	.002
Eye: W/L	.62	.007	.59	.005	3.884	.001
MDE/ID	2.36	.032	2.26	.025	2.476	.023
Ant. I L/Head W	.59	.011	.48	.004	9.890	<.001
Ant. III L/Head W	.31	.005	.26	.003	21.279	<.001
Pron.: W/L	.86	.012	.88	.019	-.949	.355
Foretib. L/Pron. L	1.46	.024	1.25	.017	7.166	<.001
Hindtib. L/Pron. L	2.03	.033	1.88	.024	43.862	<.001

^a W = width, L = length, MDE = maximum distance across head at eyes, ID = interocular distance on front.

female in having larger eyes and longer antennae and legs. As indicated in Table 1, the male eye is both wider and more prominent than in the female. The degree of dimorphism of the eyes, as reflected in the ratio MDE/ID, is comparable to that in the *Tenuicostatis* Group of *Pyrota* (Selander, 1983). Mean ratios for the two sexes are nearly identical to those in *P. tenuicostatis* (Dugès), which, like *W. aratae*, is apparently strongly nocturnal. Greater mean length of antennal segments I and III in the male is established in Table 1 on the basis of sexual comparison of the ratios of length of these segments to the width of the head. The magnitude of the sexual difference in leg length is indicated using the ratios of the lengths of the fore- and hindtibia to the length of the pronotum. Mean relative foretibial length is 17% greater in the male than in the female; the comparable value for the hindtibia is 8%.

As shown in Table 1, there is no significant sexual dimorphism in the ratio of width to length for either the head or pronotum.

In the description of the adult given above maxillary palpal segments designated III and IV are, respectively, the penultimate and ultimate. I have for some time incorrectly regarded the meloid maxillary palpus as being 3-segmented. Segments designated II and III in some of my previous papers are, properly, III and IV. (I refer here specifically to free palpal segments; if Schneider (1981) is correct in asserting that the fixed palpifer on the dorsal surface of the body of maxilla is a true palpal segment, the palpus is actually 5-segmented.)

SYNONYMY

Genus *Wagneronota* Denier

Wagneria Denier, 1932: 90; 1933: 241.

Wagneronota Denier, 1935a: 26 [New name for *Wagneria* Denier (1932), preoccupied in Diptera]. Kaszab, 1959: 77.

Type-species: Lytta aratae Berg; fixed by original designation and monotypy.

Wagneronota aratae (Berg)

Lytta aratae Berg, 1883: 66 [Holotype (unique), male, from Mendoza Province, Argentina, Brachmann, in Berg Collection, Museo de La Plata, examined].

Epicauta aratae, Bruch, 1914:403.

Wagneria aratae, Denier, 1932: 91–92, figs. c–g.

Wagneronota aratae, Denier, 1935b: 170. Hayward, 1960: 23. Viana and Williner, 1972: 16; 1973: 15.

Wagneronota aratai [sic], Bosq, 1943: 12. Kaszab, 1959, fig. 2.

SYSTEMATIC POSITION OF *WAGNERONOTA ARATAE*

Denier (1932) noted an affinity between *Wagneronota* and *Pyrota* but suggested an even closer relationship between *Wagneronota* and the Old World *Cyaneolytta* Péringuey. Kaszab (1959, 1969) included *Wagneronota* in the Pyrotini, where the genus is shown in his phylogenetic tree (1959) as the closest relative of *Pyrota*. While adults of *Cyaneolytta* have the slender body form of *Wagneronota* and in many species attain relatively large size, I see no real basis for postulating a special relationship between the two genera. For one thing, *Cyaneolytta* has none of the male secondary sexual modifications found in *Wagneronota*. Moreover, as Kaszab (1959) has shown, *Cyaneolytta* is typically lyttine in that vein M_2 in the apical region of the hindwing arises at the juncture of media with cubitus rather than further anteriorly, at the point where the vertical vein meets the base of media. On the other hand, whether one considers sexual behavior, larval anatomy, or adult anatomy, *Wagneronota* is basically very similar to *Pyrota*.

Kaszab (1959) did not justify his phylogenetic arrangement of the pyrotine genera, which in my opinion seems quite arbitrary. I know of no derived characteristic shared only by *Wagneronota* and *Pyrota* that would justify isolating these genera from the other pyrotines, and on a purely phenetic basis it is by no means evident that *Lyttamorpha* Kaszab and *Glaphyrolytta* Martínez are more distant from *Pyrota* than is *Wagneronota*. In fact, *Lyttamorpha* and *Glaphyrolytta* more closely resemble *Pyrota* in characters of the male genitalia and abdomen than does *Wagneronota*.

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